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RESEARCH ARTICLE

Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants

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Abstract

Context Intact tropical rainforests are considered robust to plant invasions. However, land-use change alters the structure and species composition of native forest, opening up tropical landscapes to invasion. Yet, the relative roles of key drivers on tropical forest invasions remain little investigated.

Objectives We examine factors affecting plant invasion of rainforest remnants in oil-palm dominated landscapes in Sabah, Malaysian Borneo. We hypothesized that invasion is greater in highly fragmented

landscapes, and in disturbed forests with lower native plant diversity (cf. old-growth rainforests).

Methods Native and exotic plants were surveyed in 47 plots at 17 forest sites, spanning gradients in landscape-scale fragmentation and local forest disturbance. Using partial least squares path-modelling, we examined correlations between invasion, fragmentation, forest disturbance, propagule pressure, soil characteristics and native plant community.

Results We recorded 6999 individuals from 329 genera in total, including eight exotic species (0–51% of individuals/plot, median = 1.4%) representing shrubs, forbs, graminoids and climbers. The best model ($R^2 = 0.343$) revealed that invasion was correlated with disturbance and propagule pressure (high prevalence of exotic species in plantation matrix), the

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latter being driven by greater fragmentation of the landscape. Our models revealed a significant negative correlation between invasion and native tree seedlings and sapling community diversity.

Conclusions Increasing landscape fragmentation promotes exotic plant invasion in remnant tropical forests, especially if local disturbance is high. The association between exotic species invasion and young native tree community may have impacts for regeneration given that fragmentation is predicted to increase and so plant invasion may become more prevalent.

Keywords Agricultural landscapes · Forest degradation · Fragmentation · Non-native species · Oil palm · Structural equation modelling

Introduction

Exotic species invasion is recognised as a major agent of environmental change across all ecosystems (Sala et al. 2005). Invasion is considered to be a function of four factors: propagule pressure, the abiotic characteristics of the invaded system, and the biotic characteristics of both the invaded system and invading species, all of which can be altered by human activity (Pyšek and Richardson 2006). In a given invasion scenario these factors contribute to varying degrees, and it is crucial to identify the relative role of each in driving invasion in a particular ecosystem (Catford et al. 2009). Many temperate forests are highly invaded by exotic plants due to historic land-use change causing substantial forest cover loss and resulting in highly fragmented and disturbed landscapes (McNeely 1995; Williams 2003; Haddad et al. 2015). Conversely, intact, lowland, humid tropical forests are usually considered to be robust to plant invasions due to low propagule pressure, low forest disturbance and because exotic species typically do not thrive in the strongly shaded conditions within undisturbed forests (Fine 2002; Denslow and DeWalt 2008). In addition, it has been hypothesised that the typically high native diversity in tropical rainforests means there are fewer empty niches, providing biotic resistance to invading exotic plants (Fine 2002; Denslow and DeWalt

2008). However, land-use change is impacting large tracts of forest across the tropics (Pütz et al. 2014; Haddad et al. 2015; Qie et al. 2017), opening up these landscapes to exotic propagules and further disturbance in the remaining patches of forest (Hulme 2009). Forest degradation alters the availability of light and other resources, changing the nature of inter-specific competition (Denslow and DeWalt 2008; Carson and Schnitzer 2011), and potentially exposes these forest patches to invasion of exotic plants. Yet, despite this, little is known about plant invasions within human-modified tropical landscapes (Kueffer et al. 2013), including remnant forests which are crucial for maintaining local and regional native biodiversity.

Large-scale deforestation in the tropics is predominantly driven by expansion of agriculture, and these agricultural areas have high levels of disturbance and abiotic conditions which differ from those of intact tropical forests (Malhi et al. 2014; Curtis et al. 2018). Abiotic conditions in tropical agricultural areas (e.g. high light levels, high temperature, low humidity, altered soil nutrients and pH) promote establishment of ruderal exotic plant species that are transported and introduced by humans via extensive networks of roads (With 2002; Von der Lippe and Kowarik 2007; Padmanaba and Sheil 2014; Fee et al. 2017), resulting in exotic-rich weed-covered banks along disturbed roadsides (Fee et al. 2017). These highly disturbed agricultural areas provide an on-going source of propagules and may promote invasion of natural forest remnants embedded within these landscapes. From the few studies of plant invasions within humid tropical forests, the presence of exotic species correlates with variables that are associated with propagule pressure, including distance from source population and to forest edge (Edward et al. 2009; Dawson et al. 2014). If propagule pressure is high enough, seed swamping of new environments can result in successful exotic establishment, regardless of whether the conditions of the invaded system are ideal for that species (see Propagule pressure hypothesis; Lockwood et al. 2005; Colautti et al. 2006). Nonetheless, abiotic and biotic factors also contribute to the invasion process.

Disturbance has been foundational in the formulation of several invasion hypotheses (e.g. Disturbance, Habitat filtering, Empty niche and Increased Resource

Availability hypotheses; see Catford et al. 2009 for invasion hypothesis overview), therefore invasion is expected to be higher in the most disturbed tropical rainforests. Commercial selective logging and the impact of fragmentation (e.g. via edge effects) alter the structure of remaining rainforest due to timber removal and disturbance-related tree mortality (Laurance et al. 2002; Malhi et al. 2014; Gibbs and Salmon 2015). The reduction in canopy cover increases light in the forest understorey, which affects the abiotic conditions of remnant forest patches, when compared with continuous, undisturbed forest (Laurance et al. 2002). Gradients from forest edge to interior have been recorded for temperature, humidity, wind intensity and soil erosion, with the most extreme differentiation seen at forest edges, known as edge effects (Laurance et al. 2002). In disturbed tropical forests, more exotic plants have been recorded at forest edges, driven by a combination of increased propagule pressure and increased canopy openness and soil disturbance associated with forest edge conditions and anthropogenic influence (Peters 2001; Harper et al. 2005; Edward et al. 2009; Dawson et al. 2014; Döbert et al. 2017). However, these studies only looked at a few forest sites, only one studied a gradient of disturbance (Döbert et al. 2017) and none have considered gradients in landscape fragmentation.

In addition to forest structural changes caused by logging and fragmentation, changes to species community composition also occur due to disruption of native species interactions (Laurance et al. 2011; Arellano-Rivas et al. 2016). For example, removal of large timber trees and isolation from larger tracts of forest reduce the regeneration of native old-growth tree species through reduced fruiting and dispersal events, shifting tree species composition to earlier successional states with lower community-average wood density (Laurance et al. 2006; Lôbo et al. 2011; Pütz et al. 2014; Gibbs and Salmon 2015; Qie et al. 2017). The negative impacts of fragmentation on native species communities are greater in small, isolated fragments and accumulate over time (Gonzalez 2000; Ferraz et al. 2003; Hill and Curran 2003; Haddad et al. 2015), with the understorey tree community strongly affected due to adult trees producing fewer viable seeds (i.e. extinction debt; Stride et al. 2018). Therefore, forest remnants may be particularly vulnerable to invasions due to reduced biotic resistance arising from the loss of native forest

species. However, evidence for biotic resistance to exotic plant invasion in tropical rainforests is limited (Fine 2002; Levine et al. 2004; Denslow and DeWalt 2008), with no consensus currently (Teo et al. 2003; Brown et al. 2006). Thus it is still unclear whether biotic interactions between native and exotic species (i.e. biotic resistance from the native community as well as suppression of native growth by invading exotic species) play a significant role in mediating invasion of tropical forests.

South-East Asia has the highest rates of deforestation (Achard et al. 2002; Sodhi et al. 2004) and logging (primarily trees from Dipterocarpaceae; Hansen et al. 2008; Lewis et al. 2015; Brearley et al. 2016) in the world (Bryan et al. 2013; Gaveau et al. 2017), due in particular to the expansion of oil palm (*Elaeis guineensis* Jacq.) cultivation in Malaysia and Indonesia in recent decades. This expansion of agriculture results in a highly fragmented forest landscape made up of commercial oil palm plantations with uncultivated, often heavily logged forest remnants (Reynolds et al. 2011). These remnant forests are therefore usually highly degraded and contain reduced assemblages of both plants and animals, compared with old-growth continuous forest, particularly if very little core forest area remains within the remnants (Lucey et al. 2017). However, these forest remnants can be important for conserving biodiversity and ecosystem services and for connecting forest patches within oil palm dominated regions, even if they are highly degraded (Yeong et al. 2016; Lucey et al. 2017; Scriven et al. 2017; Fleiss et al. 2020).

In this study, we examine the relative influence of fragmentation, forest disturbance, propagule pressure, soil characteristics and native community composition on exotic plant invasions of forest remnants within oil palm-dominated landscapes in Sabah, Malaysian Borneo. Studies examining invasion of tropical forests are rare, and this study is the first to examine a range of environmental and ecological factors leading to invasion of forest remnants embedded within an oil palm landscape. We use partial least squares path modelling (PLS-PM) to test the expectation that invasion is positively correlated with landscape-scale fragmentation, local forest disturbance and propagule pressure, and negatively correlated with native community diversity, whilst accounting for soil characteristics. We also expect the native community to respond negatively to land-use change.

Material and methods

Study sites

Between July and October 2017, we sampled 47 plots within 17 sites distributed widely across the state of Sabah, Malaysian Borneo (Fig. 1a). Sites were selected to span a wide gradient of fragmentation and disturbance, including isolated, heavily logged, small forest remnants (< 15 ha) that were fully surrounded by oil palm, as well as larger, heavily

logged forest remnants (> 100 ha) that were connected at the plantation boundary to larger tracts of government protected forest. Forest sites in oil-palm dominated landscapes ($n = 13$ sites), which have between 1 and 64% natural forest cover remaining within a 2 km radius buffer surrounding study plots (see section below; characterising fragmentation), were compared with four sites within an extensive tract of intact ‘continuous’ logged and unlogged protected forest (> 1 million ha; Fig. 1a). These continuous forest sites provided baseline data for

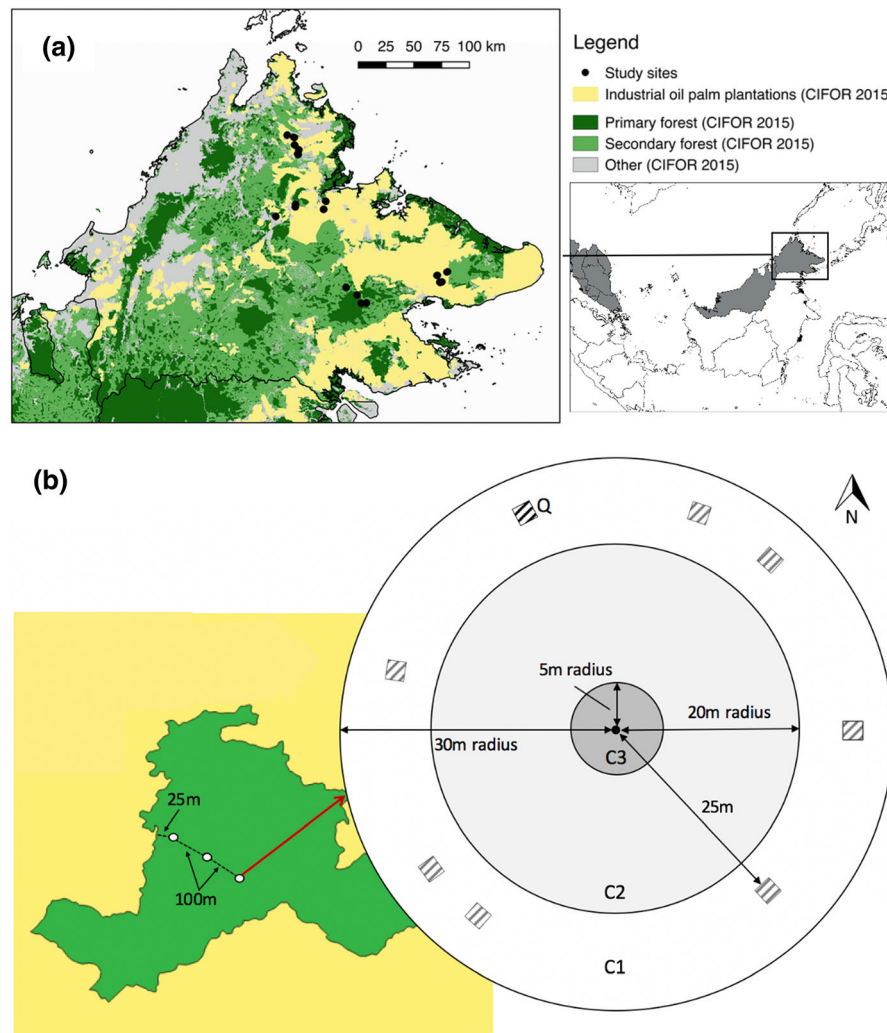


Fig. 1 **a** Map of study locations, forest cover and industrial oil palm plantations within Sabah, on the island of Borneo (inset). **b** Schematic diagram of experimental plot design within fragmented and continuous forest sites. Distance of plots from forest edge and between plots are shown along with the radiuses of each plot and subplot, and location of quadrats.

Measurements are as follows: C1 = trees ≥ 25 cm DBH; C2 = trees 10–25 cm DBH; C3 = tree saplings 2–10 cm DBH and Q = tree seedlings (< 2 cm DBH) and other ground vegetation (including shrubs, forbs and grasses). See text for full details on floristics surveys. CIFOR forest cover dataset available at Gaveau, Salim and Arjasakusuma (2017)

comparison of forest remnants within an oil palm landscape and also represented variation in levels of forest disturbance in the region, including both fully protected unlogged forest ($n = 2$) and commercially logged sites ($n = 1$ site in once-logged forest; $n = 1$ site in twice-logged forest). Thus, our choice of sites spanned a gradient in the degree to which the landscape surrounding our sites was fragmented as well as the intensity to which the forest areas were previously commercially selectively logged.

Sites within oil palm plantations were conservation set-asides, and the majority were managed as sites with ‘High Conservation Values’ (HCVs, Senior et al. 2015), which the plantations retain and manage as part of the Roundtable on Sustainable Palm Oil (RSPO) certification process for sustainable palm oil (RSPO 2018). These sites were selectively logged to varying degrees in the 1990s prior to oil palm cultivation (see details below on disturbance quantification) and were generally unsuitable for planting oil palm (i.e. too steep or too rocky). Study sites were at least 1 km apart to avoid spatial autocorrelation. The maximum distance between sites is c. 192 km with elevation range from 42–267 m above sea level, hence we do not expect the climate to vary greatly between sites.

Plot-level surveys of native and exotic plants

We surveyed plants in two or three circular plots (30 m radius; 0.28 ha) per site, depending on forest extent at each site, with only two in the smallest remnants (< 12.5 ha; n sites = 4). We used a four-level nested approach to sample plants within different size classes (Fig. 1b). The diameter-at-breast height (DBH) was recorded for all large trees ≥ 25 cm DBH within the 0.28 ha plot (Fig. 1b; C1), all small trees 10–25 cm DBH within a sub-plot of 20 m radius (Fig. 1b; C2), and all tree saplings 2–10 cm DBH within a sub-plot of 5 m radius (Fig. 1b; C3). Tree seedlings and other ground vegetation (forbs, shrubs, climbers, ferns and graminoids, from herein referred to simply as ground vegetation) were surveyed in eight 1×1 m quadrats (Fig. 1b; Q) located 25 m from the plot centre along eight randomly chosen bearings. Within each of these quadrats, we recorded all plants (tree seedlings, shrubs, climbers, forbs, graminoids and ferns) rooted inside the quadrat, and ≤ 2 cm DBH. We considered an individual as a plant with a distinct root system; for adult trees, tree saplings and

tree seedlings individuals were straightforward to distinguish. All ground vegetation, including clonal species (e.g. graminoids and climbers) that can appear as distinct individuals above ground yet connected below ground, was manually removed from the soil to determine number of individuals for each morpho-genus, with unknown individuals taken as vouchers for identification. Adult trees and saplings were identified to genus in the field by an experienced local botanist (co-author AJ). Voucher specimens and photographs of plants in the quadrats were used to identify individuals by a botanist at Danum Valley Field Centre (co-author BBO) and the herbarium at the Forest Research Centre, Sepilok. Exotic species were identified based on lists and guides of Sabah’s known exotic plants prepared prior to fieldwork (see Pallewatta et al. 2003; Bakar, 2004; Peh, 2010; Döbert et al. 2017; Fee et al. 2017; CABI 2017) and confirmed by botanists from vouchers. The observed number of exotic species and number of exotic stems per plot were used as measurements of invasion within a plot. All analyses were carried out at plot-level, and at the level of genus, due to the challenges of reliably identifying native plants to species level in diverse tropical forests. Exotic plants were identified to the species level.

Quantifying the native community

We computed two measures of native community alpha diversity; observed genus richness and Faith’s phylogenetic diversity (PD; Faith 1992). Faith’s PD is the total sum of phylogenetic branch lengths between species—we chose this measure because it is intended to capture the evolutionary signal in functional traits and as such is associated with functional diversity and can be a valuable predictor of ecosystem-level responses (Flynn et al. 2011). These diversity metrics were calculated per plot ($n = 47$) for the total dataset and separately for trees, saplings, seedlings and the ground vegetation. Individuals that could not be identified to genus ($n = 17$; $< 1\%$ of all stems) were removed from the dataset prior to phylogenetic analyses. A phylogeny was created using Phylomatic v.3 (Webb and Donoghue 2005; available at <https://phylodiversity.net/phylomatic/> [accessed 4 May 2018]) and a pruned version of the Angiosperm Phylogeny Groups APGIII maximally resolved supertree of angiosperms (R20120829). Two genera could not

be included in the phylogeny, as they were not part of the original supertree, leaving 303 genera for inclusion. The phylogeny was rooted and branch lengths were based on node ages (most recent common ancestor) of Wikstrom et al. (2001) and estimated using the 'BladJ' algorithm in Phylocom (Webb et al. 2008). From the resulting phylogeny, phylogenetic diversity (PD; the sum of the total branch lengths measured in millions of years; Faith 1992) was calculated using the 'picante' package (Kembel et al. 2010) in R Studio 2.14 (R Core Team 2019).

Characterising fragmentation, disturbance, propagule pressure and soil

We measured forest fragmentation in the surrounding landscape by quantifying the area of forest and non-forest habitat (m^2) within a 2 km radius buffer surrounding each plot. This buffer is a proxy for the dispersal potential of native forest species (i.e. more forest in the buffer would likely indicate a higher presence of mother trees as well as pollinators and animal dispersers). This buffer included forested areas not connected to forest remnants where plots were carried out, as well as connected forest within which the plots were embedded. Quantification of buffer habitat was carried out using drone images provided by plantation managers taken during May–November 2016, after which we assume no or negligible change to forested area within plantations had occurred before fieldwork took place (July–October 2017), due to protections in place. Plots in 'continuous' sites were almost entirely forest, but the tract of continuous forest nonetheless contains some small settlements (i.e. field research centre) and so there were small areas of non-forest ($< 0.5\%$) in buffer zones around these plots. Within the 2 km buffer, the amount of forest edge in the landscape was also calculated using the 'rgeos' and 'raster' packages (Hijmans and van Etten 2012; Bivand and Rundel 2013), and was equal to the number of raster grid cells ($5 \times 5 \text{ m}$) the forest edge passed through. A unitless index of edge density was calculated for each plot as the area of edge cells divided by the area of forest cells. This edge density index was a proxy for the amount of edge habitat in the landscape that would likely be highly degraded based on edge effects. The time since fragmentation was calculated from the year of first planting of oil palm

(between 1991 and 2009) as provided by estate managers.

At all sites, we derived two proxy variables for local forest community structure and recovery since disturbance (primarily the result of previous commercial selective logging, except at the two unlogged 'continuous' sites). These two variables were: (i) the number of large stems ($> 25 \text{ cm DBH}$) belonging to the tree family Dipterocarpaceae, which comprises $\sim 22\%$ of tree species and 61% of biomass in the region (Slik et al. 2003; Saner et al. 2012), and provides a useful comparison between disturbed remnants and unlogged 'continuous' forest; and (ii) average plot-level wood density for trees $> 10 \text{ cm DBH}$ was calculated, because wood density can be an indicator of successional status in forest species (Slik et al. 2008; Feeley et al. 2011; Qie et al. 2017). Wood density was calculated for each genus using the 'BIOMASS' package in R (Réjou-Méchain et al. 2017), based on the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009).

As a direct proxy of propagule pressure, exotic plant species richness and abundance were measured along two 100 m transects located within the oil palm matrix at each site. The first transect was along the roadside of a major unpaved plantation road (lorries and car traffic) and the second at the oil palm-forest edge, either along an unpaved minor road (mostly motorbike traffic) or oil palm terrace track (pedestrians). Along both 100 m transects, the presence/absence of 18 exotic species were recorded in each 1 m section and 1 m either side of the transect line (i.e. 2 m^2 sections). Exotic species richness was computed as the total number of exotic species (out of 18) recorded across these two transects. Exotic species abundance was the total number of 1 m transect sections ($n = 100$ per transect) that species were present in, and total abundance of all exotics was computed across the two transects (i.e. out of 18 species \times 200 sections = 3600).

To measure soil available phosphorus and pH the topsoil was sampled in each plot (20 cm core; $n = 5$ per plot: one at the plot centre and four 15 m from centre in each of the cardinal directions). After drying (at 50°C) soil samples were thoroughly mixed and sub-sampled for analyses at plot level ($n = 47$). Soil chemistry was analysed at the Forest Research Centre, Sepilok, Sabah. Available phosphorus was extracted using water and measured using the molybdenum-blue

method and read at 880 nm on a spectrophotometer (following Anderson and Ingram 1994). Soil pH was measured with a combination glass-calomel electrode in a 1:2.5 ratio of soil to deionised water.

Data analysis

We analysed the relative importance of different factors in invasion using partial least squares path modelling (PLS-PM; see Table 1 for a summary of variables and Supporting Information Appendix S1 for full details on PLS-PM method and variable selection) using the ‘plspm’ R package (Sanchez and Trinchera 2012; see Waddell and Chapman 2020 for the R code). PLS-PM is a variance-based structural equation modelling method, which fits multiple regressions using measured and latent variables connected in a pathway reflecting ecological theory (Sanchez 2013). Latent variables are those which cannot be observed or directly measured but are of conceptual interest and are indicated by their associated measured variables, which comprise at least two highly correlated measured variables. Some measured variables were

transformed (Table 1) to improve normality, in accordance with modelling assumptions (SI Appendix S1). All measured variables were centred and scaled (mean of 0 and variance of 1) prior to input into the PLS-PMs to assist with model convergence and interpretation.

All models were developed starting from the full specification in Fig. 2 and removing non-significant terms in a stepwise manner until all retained links were statistically significant ($P < 0.05$; Sanchez, 2013). Two-sided P -values for standardised path coefficients (i.e. the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable) were estimated by 10,000 bootstrap estimations. In ‘plspm’, site identity cannot be included as a random effect, so site effects were accommodated by taking bootstrap samples at the level of site, i.e. bootstrap samples were made by randomly selecting sites and all their constituent plots, with replacement.

We first fitted the model on the full dataset, i.e. where native community diversity comprised recorded native plants of all size classes. We then fitted separate

Table 1 Measured variables included in the structural equation models

Latent variable	Measured variable	Details	Transformation
Fragmentation	Area of non-forest	m ² within 2 km buffer	Untransformed
	Edge density	The amount of forest edge/forest area within 2 km buffer	Untransformed
	Age	years since fragmentation	ln + 1
Disturbance	Number of large dipterocarps	Number of large stems (> 25 cm DBH) per plot	(sqrt)* – 1
	Wood density	average wood density of adult trees (> 10 cm DBH) per plot	(log10)* – 1
Soil characteristics	Soil pH	Average pH of five 20 cm soil cores	log10
	Available phosphorus (P)	Average available P of five 20 cm soil cores	log10
Propagule pressure	Exotic richness outside	Number of exotic species along two transects, in oil palm matrix	Untransformed
	Exotic abundance outside	Abundance of exotic species along two transects, in oil palm matrix	Untransformed
Native community	Native genera richness	Observed genera count per plot	Untransformed
	Native abundance	Observed number of individuals per plot	Untransformed
	Native phylogenetic diversity	Faith’s phylogenetic diversity per plot	Untransformed
Invasion	Exotic genera richness	Number of exotic genera per plot	ln + 1
	Exotic abundance	Number of exotic stems per plot	ln + 1

Including details of each variable, transformations used to prepare data for analysis and which latent variables are indicated by each measured variable. Abbreviations are: log10 = base 10 logarithm, ln + 1 = natural log + 1 and sqrt = square root. Measured variables which were multiplied by minus one, to ensure the latent variable reflected the processes we labelled them with, are indicated by *– 1

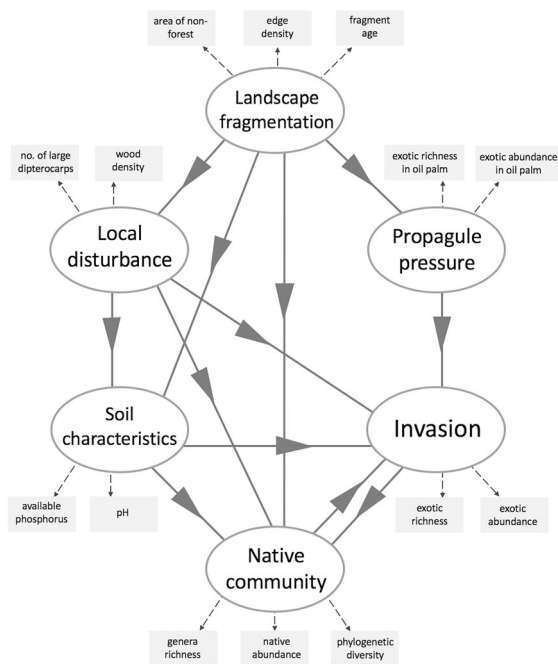


Fig. 2 Hypothetical partial least squares path model showing the relationships between fragmentation, disturbance, propagule pressure, soil characteristics and native plant diversity on invasion within of lowland tropical forests. Latent variables are shown in ovals and the measured variables in rectangles. Measurement model is represented by the dashed lines and the structural model is represented by the solid lines. Models were tested in both directions for the relationship between native community and invasion indicated by the double arrows. Full details on these variables are in Table 1 and within the text

PLS-PMs for native adult trees, tree saplings, tree seedlings and ground vegetation to test whether different subsets of the native community were more strongly correlated with invasion. As we do not know the directionality of the relationship between native community diversity and invasion, we tested all models in both directions for this relationship. In all cases, models were assessed for validity and reliability in both the measurement and structural model (see SI Appendix S1 for details on PLS-PM model evaluation).

Results

In the 47 plots we surveyed a total of 6999 individuals (SI Table S2) from 329 genera, including eight exotic species, ranging from 0 to 7 species (median = 1) and 0–51% of stems (median = 1.4%) per plot. Exotic

species included shrubs, forbs, graminoids and climbers (there were no exotic trees). The most abundant exotic was a common tropical exotic shrub, *Clidemia hirta* (Melastomataceae), which made up 73.8% of all exotic stems (SI Table S3). The second most common exotic was also a shrub, *Chromolaena odorata* (11% of exotic stems), and the other six species were either forbs, climbers or a graminoid (1–4% of exotic stems).

Overall, native richness ranged from 18–69 genera/plot (median 45) with plots in the 13 oil palm remnant sites having lower richness (median of 42 genera/plot; range 18–69) compared with continuous sites (median of 46.5 genera/plot; range 39–57). In continuous sites the most common native genus amongst adult trees was *Shorea* (Dipterocarpaceae), for saplings *Mallotus* (Euphorbiaceae), for seedlings *Shorea* (Dipterocarpaceae) and for ground vegetation *Selaginella* (Selaginellaceae). By contrast in the oil palm remnant sites, the most common native genera were *Ficus* (Moraceae), *Hopea* (Dipterocarpaceae), *Glochidion* (Phyllanthaceae) and *Selaginella* (Selaginellaceae) for the same size classes, respectively.

The final PLS-PMs (Figs. 3, 4, S1 and S2) explained 34% of the variation in invasion, 74% of variation in propagule pressure, between 26 and 53% of native community diversity and 55% of soil characteristics (all of which are latent variables informed by 2–3 measured variables). There was strong evidence in support of our final PLS-PMs in terms of the reliability and validity of the measurement model and an adequate fit of the structural model (see Appendix S1 and Tables S4–6 for full details on model evaluation).

Drivers of invasion

After removal of non-significant terms, the best model with the full native community (i.e. combining data for native adult trees, saplings, seedlings and ground vegetation; Fig. 3), found a strong direct positive correlation between propagule pressure and invasion ($P < 0.001$), with a strong indirect positive correlation of fragmentation ($P < 0.01$) on invasion via increased propagule pressure. Forest disturbance also had a direct positive correlation with invasion ($P < 0.05$), but there was no significant effect of total native community diversity or soil characteristics ($P > 0.05$) on invasion.

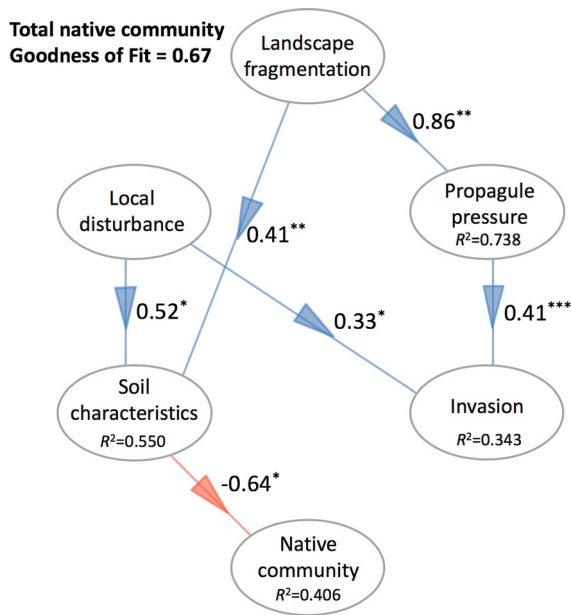


Fig. 3 Fitted partial least squares path model showing the relationships between fragmentation, disturbance, propagule pressure, soil characteristics and native plant diversity on invasion within of lowland tropical forests. The model was simplified from the specification in Fig. 2 by removing non-significant effects. The goodness-of-fit index for the model and R^2 values for the endogenous latent variables are displayed. Standardised path coefficients and P -values were estimated by 10,000 bootstrap estimations. Standardised path coefficients are shown next to arrows, red indicates a negative correlation and blue a positive correlation. They denote the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable. P -values: * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$

Models accounting separately for native adult trees, saplings, seedlings and ground vegetation communities did not support a role of native community diversity on invasion (native \rightarrow invasion; Fig. S1 and Table S7). However, when the direction of the biotic relationship in the model was reversed, i.e. invasion \rightarrow native, we found significant negative effects of invasion on native tree sapling and tree seedling communities (Fig. 4; tree saplings: standardised path coefficients = -0.348 , $P = 0.012$, $R^2 = 0.4$; tree seedlings: standardised path coefficients = -0.28 , $P < 0.01$, $R^2 = 0.299$). In these models, there was no significant effect of invasion on the total native community, adult trees or ground vegetation (Fig. S2).

Responses of the native community to land-use change

The exotic and native communities (both total and subsets) responded differently to disturbance and fragmentation (Figs. 3, 4, S1 and S2). The total native community was indirectly correlated negatively with both fragmentation and disturbance, via their positive influence on soil characteristics (i.e. higher native diversity and abundance when there was low soil pH and available soil phosphorus; Fig. 3 and Table S7). Instead, invasion was positively correlated with these land-use change variables, as we hypothesised. In the native subsets (Figs. 4, S1 and S2, and Table S7), adult tree and tree sapling communities were directly negatively correlated with disturbance, tree seedling community was directly negatively correlated with fragmentation, and the ground vegetation community (forbs, shrubs, climbers, ferns and graminoids) was indirectly negatively correlated with both fragmentation and disturbance, via interactions with soil characteristics. Hence, all the native community subsets (adult trees, tree saplings, tree seedlings and ground vegetation) were negatively associated with disturbance and fragmentation.

Discussion

Our study found that a higher degree of landscape fragmentation leads to higher invasion of exotic plant species in forest remnants, due to a greater source population of exotic plants found in the anthropogenic (i.e. plantation) areas of these landscapes. In contrast, we found little effect of soil characteristics and the native community on exotic invasion, but a negative influence of exotic invasion on the native tree sapling and seedling communities.

Fragmentation drives propagule pressure to increase invasion

Landscape fragmentation (i.e. lower forest cover, more edge habitat and a longer history of forest clearance) promotes higher invasion of the oil palm matrix (planted areas and roads), which increases the likelihood of remnant forests being invaded by exotics due to increased propagule pressure. We expected that greater numbers of exotic species would have

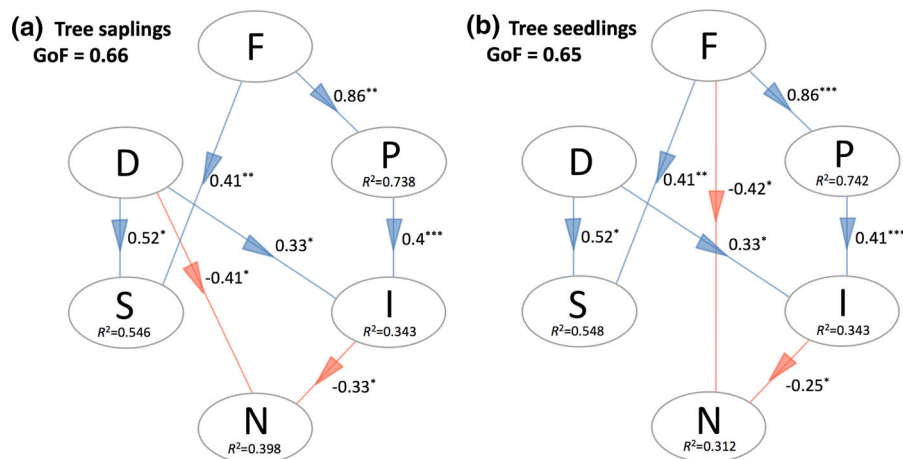


Fig. 4 Partial least squares path model showing the relationships between fragmentation, disturbance, propagule pressure, soil characteristics and invasion on **a** native tree sapling and **b** native seedling diversity. The model was simplified from the specification in Fig. 2 by removing non-significant effects. The goodness-of-fit index (GoF) for each model and R^2 values for the endogenous latent variables are displayed. Standardised path coefficients and P -values were estimated by 10,000 bootstrap

estimations. Standardised path coefficients are shown next to arrows, red indicates a negative correlation and blue a positive correlation. They denote the extent of standard deviation change of one latent variable attributed to one standard deviation change to another latent variable. P -values based on 10,000 bootstrap estimations: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. F fragmentation, D disturbance, P propagule pressure, S soil characteristics, N native community and I invasion

established in the oil palm matrix because of enhanced transport of propagules (Ansong and Pickering 2013) and the higher availability of resources brought about through disturbance, which would promote colonisation by exotic species (Fee et al. 2017). Small, isolated forest remnants that are completely surrounded by oil palm, or other agricultural areas (c.f. those contiguous with larger tracts of forest) may therefore have more exotic propagules arriving from all directions, facilitating the invasion process. Although exotic invasions have not yet been thoroughly examined in fragmented tropical rainforests, similar patterns to those in this study have been reported in many natural habitats within fragmented landscapes, with invasion highest in small, isolated remnants (Vilà and Ibáñez 2011). We conclude that propagule pressure, driven by fragmentation, is the main factor influencing invasion of exotics in our study (based on total effect sizes in Table S7), however, invasion is generally low unless there is high local disturbance of the forest.

Increased invasion in disturbed forests

We found that invasion is more likely in forests with high levels of previous disturbance, represented by those with fewer large dipterocarp trees and lower

average wood density, indicative of forest regressing to an early successional state. The strong positive relationship between disturbance and invasion is likely to indicate increased resource availability (e.g. light and space) associated with commercial selective logging, providing opportunities for invading exotics to colonize. The correlation between invasion and increased resource availability following disturbance is found across many habitats and disturbance regimes (natural and anthropogenic), and underpins several invasion hypotheses (Davis et al. 2000; Hood and Naiman 2000; Colautti et al. 2006). In tropical forests, increased light levels following selective logging can also lead to increases in native pioneer species and native weeds (Catford et al. 2009; Lockwood et al. 2013) and these environmental factors are likely to be instrumental in driving the invasion of exotic species observed in our data. Therefore, fragmentation and disturbance may operate synergistically; land-use change may bring exotic species propagules into the oil palm matrix, but these exotic species will only establish in the remnant forests if local conditions are suitable and disturbance promotes these conditions.

Little evidence for biotic interactions

We found no signal of biotic resistance to invasion from the native community in our results when the models specified an effect of the native community on invasion, which is in line with wider meta-analysis of terrestrial plant invasions (Jeschke et al. 2012). However, when the models specified an effect of invasion on the native community, we found significant negative correlations between invasion and native tree sapling and seedling communities. This may indicate either the impact of a dominant exotic inhibiting native recruitment or be driven by indirect effects of land-use change on these cohorts of native trees (i.e. indirect effect of the disturbance latent variable on saplings via invasion and similarly fragmentation on seedlings).

These findings may be explained by young native trees and exotic shrubs (~ 85% of exotic stems) having higher niche overlap than other components of the native community (i.e. adult trees and ground vegetation) because they have a similar woody habit and occupy the same lower understorey environment. Exotic species may have disrupted the recruitment of current tree saplings and seedlings, which would have been young saplings or seeds when exotic species first invaded these forests post-fragmentation (8–26 years before sampling), by outcompeting them for resources. The dominant exotic recorded in this study, *Clidemia hirta* (74% of exotic individuals), exhibits functional traits associated with high competitive ability (e.g. high seed number, fast growth rate, early age of reproduction, asexual reproduction, fruits produced year round and very large seed bank), allowing for rapid population growth (Rejmánek and Richardson 1996; Singhakumara et al. 2000; Daehler 2003), making it a highly invasive species and a pest throughout most of its introduced range (Wester and Wood 1977; Gerlach 1993). Similar patterns have been observed in temperate forests with dominant invasive species disrupting native seedling growth (Gorchov and Trisel 2003; Stinson et al. 2006), and in selectively logged Malaysian tropical rainforests, Döbert et al. (2017) found fewer Dipterocarpaceae seedlings where exotic biomass was higher. Therefore, high niche overlap may lead to strong competition between young trees and exotic shrubs for resources such as light. In addition, *C. hirta* and *Chromolaena odorata* (the second most common exotic invasive

species recorded) both have allelopathic effects, which have been shown to significantly reduce native seed germination and growth during laboratory studies (Hu and Zhang 2013; Ismaini 2015).

Our results are correlational and do not track changes in the native community over time, so inferring biotic interactions is problematic. Nevertheless, our results indicate that invasion of exotic plants is more closely associated with the lack of young native trees than other components of the native plant community (e.g. ground vegetation and adult trees) in these forests, and patterns are likely driven by *Clidemia hirta*. However, in order to determine the mechanisms driving observed biotic relationships in our data, as well as the true directionality of observed relationships, long-term manipulative field experiments would be required.

Native and exotic plants respond differently to disturbance and fragmentation

Our results suggest that different components of human land-use change correlate, at varying strengths, with different subsets of the native community (adult trees, tree saplings, tree seedlings and ground vegetation). The strong direct correlation between disturbance and native adult tree diversity could potentially be driven by the disturbance variables included in the models being derived from the adult tree community (i.e. number of large dipterocarp trees remaining and mean adult tree wood density per plot). However, as this relationship is also found with sapling diversity, a true relationship between habitat disturbance and both tree communities seems plausible. This may be due to logging decreasing diversity by the physical removal of specific species via timber extraction (i.e. dipterocarps), affecting both timber trees (adult trees) and collateral damage to other trees surrounding the extracted tree, both over- and understorey (Malhi et al. 2014). In addition, altered abiotic conditions brought about by logging practices (e.g. increased light, temperature, soil erosion) result in tree mortality and reduced fruiting in adult trees which in turn reduce recruitment (Gibbs and Salmon 2015), decreasing the richness of old-growth forest species in fragments.

The association between fragmentation and tree seedling diversity (and to a lesser extent the marginally significant correlation with tree saplings) in our data means there are fewer seedlings in areas with less

forest in the landscape, more edge habitat and in older plantations. This could reflect an extinction debt driven by pollination and dispersal limitations in highly fragmented landscapes (Ghazoul and McLeish 2001), which would have clear implications for the future regeneration of these forests (Haddad et al. 2015). Stride et al (2018) found similar results in other fragmented forest sites in our study region, with seedling richness 30% lower in forest remnants than in undisturbed old-growth forest.

The weak negative correlation between ground vegetation community composition and both fragmentation and disturbance (SI Table S7), may be due to this component of the plant community also containing light-loving native weedy species (e.g. grasses and forest edge shrubs), which act much the same as exotics in that they proliferate with disturbance (Catford et al. 2009; Lockwood et al. 2013). These native weeds could therefore dilute the relationship between native ground vegetation typical of old-growth forest and the effects of land-use change in our models. Changes in the native plant community associated with disturbance, as well as the invasion of exotic species, are likely to impact important ecosystem services in these forests, such as biodiversity, functional stability and carbon storage.

Conclusions and conservation implications

Exotic species are an understudied component of fragmented tropical landscapes, despite being an emerging threat to the natural regeneration of native tree communities within remnant forests. Indeed, three of the eight exotic species we found (*Clidemia hirta*, *Chromolaena odorata* and *Mikania micrantha*) are considered amongst the world's worst 100 invasive species due to their ability to modify the ecosystems they invade (Lowe et al. 2000), with *C. hirta* in particular, considered a pest across much of its introduced range (Wester and Wood 1977; Gerlach 1993; Peters 2001; Teo et al. 2003). Our study shows for the first time that fragmentation and local disturbance increase the invasion of exotic species in rainforest remnants within anthropogenic landscapes. Therefore, we suggest that better management to control exotic populations within oil palm plantations (e.g. along roadsides and in oil palm planted areas), along with active regeneration of forest remnants to improve

overall forest quality and canopy cover is important to reduce exotic invasions. In a natural resource management context, the way in which invasive species move through a landscape should be considered in the design of multi-functional landscapes, to ensure that these species do not undermine the conservation of forest remnants. This would involve consideration of maintaining large interior and closed canopy forests and reducing edge effects and propagule transport within the landscape. Vulnerable recovering forests in particular should be protected.

Our results highlight the consequences of fragmentation and logging on the invasion of remnant forests but also the impact on the native plant community. These findings are of critical importance given that around 80% of tropical forests are currently fragmented and/or anthropogenically modified (Potapov et al. 2017). Fragmentation is predicted to increase, with increases in the number of isolated forest remnants as well as decreases in their average size (Taubert et al. 2018) as a result of cyclical deforestation processes (i.e. deforestation and degradation making new areas of forest more accessible and susceptible to further degradation; Nowosad and Stepinski 2019). Therefore, invasion of forest remnants is likely to increase in future due to continuing deforestation, leading to changes in plant community composition and altered patterns of native regeneration, thereby potentially impacting local and regional biodiversity. Given, that maintaining regeneration of remnant forests is necessary for the sustainability of human dominated tropical landscapes, including RSPO-certified oil palm plantations (Senior et al. 2015), it is vital that the impacts of invading exotic species within these forests are properly evaluated and included in future studies.

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Author's contributions EHW, LFB, MH, JKH and DSC conceived the ideas. EHW, LFB, MH, SF, JT, JKH, CB,

YKL, ABS, AJ and DSC designed methodology; EHW, SF, ABS and AJ collected the data; BBO and AJ led plant identification; EHW and DSC analysed the data; EHW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability Data collected for this study are available to download (see Waddell et al. 2020).

Conflicts of interest Authors report no conflicts of interest.

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